

SELF-GENERATED *VERSUS* ENVIRONMENTALLY PRODUCED FEEDING CURRENTS: A COMPARISON FOR THE SABELLID POLYCHAETE *EUDISTYLIA VANCOUVERI*

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ABSTRACT

The feeding currents produced by the branchial crown of the tube-dwelling sabellid polychaete *Eudistylia vancouveri* are compared with ambient currents experienced by the *in situ* worm. The speeds of the branchial currents range between 0.025 and 0.080 cm/s and are similar to the patterns mapped by Nicol (1930) for *Sabella pavonina*. The ambient currents in contact with the branchial crown of a worm in the field are up to three orders of magnitude higher (33.6 cm/s).

When these worms are clustered together in the field, their tubes form hemispherical mounds that affect the pattern of ambient currents. Flow over the surface of the cluster is augmented in comparison to pre-cluster velocities. Thus animals within a cluster experience higher feeding currents than do solitary worms. This increase in feeding current velocity is not without potential competition for food from cluster-mates. Depletion of natural particles during the passage of a single wave through a cluster ranges from 45 to 65%.

INTRODUCTION

The mechanisms by which suspension feeding animals remove particles from the surrounding fluid is a topic of current and historical interest. Fluid movement determines to a large degree the mechanical forces impinging on an organism (*e.g.*, Wainwright and Koehl, 1976; Merz, 1984), the rates of respiration and excretion (LaBarbera, 1982), and the feeding mode employed by some organisms (*e.g.*, Lewis, 1968; Warner, 1977; Tagon *et al.*, 1980; LaBarbera, 1984). Therefore, to fully and accurately understand the feeding processes and behavior of aquatic organisms, the natural flow regime of the animal in question must be taken into account (Reidl, 1971; Vogel, 1981).

Nicol (1930) describes the morphology, ciliary tracts, and feeding currents of the sabellid polychaete *Sabella pavonina*. This very detailed work is one of the most complete descriptions of the feeding mechanisms of a polychaete (Fauchald and Jumars, 1979) and has been used as a model for other studies of sabellid polychaetes (Fitzsimmons, 1965; Lewis, 1968; Bonar, 1972). It has also been incorporated into the literature as a general model for feeding in the Sabellidae (Jørgenson, 1956, 1966; Dales, 1970; Barnes, 1980). Nicol suggests that all water movement through the branchial crown of sabellids is due to ciliary activity. However, Nicol did not account for possible effects that ambient flow may have in this process. Her observations on whole worms were carried out in small closed containers of still water; finer details were ascertained by examining excised portions of branchiae.

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Dales (1957) estimated the filtration rate (volume of material strained per unit fresh worm weight) of a variety of fan worms (sabellids and serpulids) in still water by measuring changes in the optical density of graphite particles and unicellular algal suspensions. He concluded that fan worms are "clearly . . . less efficient than other suspension-feeding invertebrates, both in the volume of water they are capable of straining, and in the kind of particles which can be retained" (p. 315). However, Warner (1977) suggested that sabellids are among the suspension feeders which can use ambient water movement to augment their own self-produced currents. Because the effect of the environmental regime has never been addressed in any study of sabellids, an important aspect of the feeding mechanisms and ecology of these animals has been neglected.

Many species within Sabellidae aggregate into densely packed nonclonal mounds (Hartman, 1969). Aggregations of tube-dwellers have been shown to affect the pattern of ambient currents (Eckman, 1979, 1983; Nowell and Church, 1979). The amount of suspended material in the water may be augmented by resuspension of particles due to the presence of tubes (Eckman *et al.*, 1981; Carey, 1983) or may be depleted by the biological activity of the tube dwellers (Fager, 1964; Woodin, 1978, 1981; Levin, 1982). None of these studies has examined these phenomena for epifaunal tubes on hard substrates.

This work examines three aspects of suspension feeding in the sabellid polychaete, *Eudistylia vancouveri*. First is a comparison of the water velocities produced by the cilia of the branchial crown with the velocities of ambient currents. Second, the effect of the dense hemispherical aggregates of worms on the water flow near the feeding crown is described. Third, removal of natural particles during a single passage of water across the surface of a worm cluster in the field is quantified.

MATERIALS AND METHODS

Field site and animal collection

Cattle Point, San Juan Island, Washington (48°27'N, 122°57'W) was the site for all *in situ* flow measurements, worm collection, and particle sampling. This rocky point extends into the Strait of Juan De Fuca and is one of the most exposed points in the San Juan Islands.

Specimens of *E. vancouveri* were collected by carefully peeling intact tubes away from the rock substrate during low tides. The animals were held in sea water tables with continuous circulation of fresh sea water. Only whole, undamaged worms were used for flow observation and measurement.

Flow observation and measurement

To measure and observe currents produced by cilia of the branchial crown, individual worms were supported upright in their natural tubes in a 15 × 10 × 20 cm clear plastic container and fresh sea water was circulated through the space between this inner container and an outer chamber to keep the inner box at ambient sea water temperature (10°–12°C).

Flow patterns produced by the branchial crown were visualized by releasing fluorescein sodium (uranine) dye (dissolved in sea water) at various locations around the worm. This dye was injected through PE-50 catheter tubing, the end of which had been drawn into a fine point (~300 μm diameter). The flow rate of the dye was controlled with a micrometer buret. The dye injection apparatus was mounted on a micromanipulator (for further details, see LaBarbera, 1981).

I observed the positions adopted by the worms at different ambient velocities using a recirculating flow tank with a variable speed motor (Vogel and LaBarbera, 1978). Worms in their natural tubes were arranged with the tubes extending into the center of the flow tank.

The velocity of ciliary currents in still water was measured with a thermistor flowmeter (LaBarbera and Vogel, 1976) modified to improve spatial resolution and to record very low velocities (see LaBarbera, 1981, for specific modifications and calibration procedure). Precision of velocity measurements was ± 0.03 cm/s; accuracy was approximately the same. The probe was 500 μm in diameter and its spatial resolution was 0.5 mm.

Current velocities within and around *in situ* clusters were measured with a portable electromagnetic water current meter (Model 511, Marsh-McBirney, Inc.). Precision of this instrument was $\pm 2\%$ of reading. The probe was 2.5 cm in diameter. An adjustable aluminum scaffolding was used to hold the flow probe securely in the desired location while readings were taken. All *in situ* velocities were recorded on a Linear Model 142 portable chart recorder. All velocities reported here are the mean (\pm S.D.) of the peak velocities of a series of waves moving through a surge channel at a particular location.

Measurement of particle depletion

To measure removal of particles from the water by a cluster of *E. vancouveri*, water samples were taken from a single wave before and after it washed through a worm cluster. To insure that the same water mass was sampled on both sides of a cluster, fluorescein dye was released upstream from the worm. A water sample was taken immediately before this marked water moved through the worm cluster, and again as it emerged from the downstream side. During sampling the water surface was never more than 3 cm above the worm tubes. Thus, these samples represent water moving through the worm cluster at crown height.

The water samples (30–80 ml) were taken with a large bore (5 mm) suction device. Each water sample was transferred to a sterile glass bottle, sealed, and stored on ice in the dark for transport to the laboratory. Elapsed time from sample collection to particle counting was less than four hours.

Three different worm clusters were sampled in this manner. To estimate the repeatability of sampling, one cluster was sampled twice (two separate waves, 20 minutes apart). At another cluster, two downstream samples were taken from a single wave.

In the laboratory, each water sample was gravity filtered through a 102 μm Nitex filter. This filtered sample was then gently inverted several times and a 2 ml subsample was removed for measurement. The precision of counts from multiple subsamples is better than 5% (B. Best, pers. comm.). The frequency distribution for 128 particle size classes was tallied and recorded by an Elzone 80XY particle counter (Particle Data, Inc.). Particle size was measured as displacement volume and is reported as the diameter of a sphere of equivalent volume. For a description of this technique, see Haven and Morales-Alamo (1970).

RESULTS

Pattern and velocities of worm-generated currents

The pattern of water movement around a fully expanded branchial crown of *Eudistylia vancouveri* in still water agrees with Nicol's (1930) description (Fig. 1B).

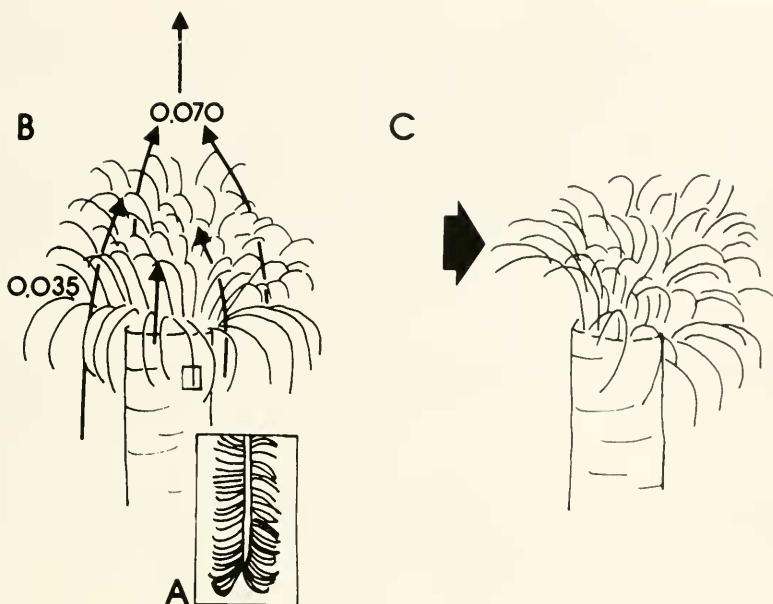


FIGURE 1. Posture of the branchial crown of *Eudistylia vancouveri* in still and moving water. (A) Enlargement of a filament and its associated pinnules. (B) Position of the filaments in still water, arrows indicate the dye streams produced by ciliary currents, the speeds of which are reported as cm/s. (C) Position of the filaments in flowing water (20 cm/s), heavy arrow shows the direction of water movement, the position of filaments and pinnules were traced from photographs.

The cilia-driven currents flow from under the branchial crown through the network of filaments. This flow is completely laminar. There is no evidence of the pulsatile flow that would result if this current were produced by the peristaltic pumping of the body within the tube. The streamlines do not mix within the branchial crown, but converge towards the midpoint above it.

Current speed at the periphery of the crown (0.5 cm above the distal tips of the filaments) ranged between 0.025 and 0.045 cm/s ($X = 0.035 \pm 0.004$ S.E.). The current speed above the center of the crown (no more than 0.5 cm from the midpoint) ranged between 0.056 and 0.080 cm/s ($X = 0.070 \pm 0.006$ S.E.). Thus the speed at the center of the crown is about twice that at the periphery. This higher speed corresponds to the larger number of cilia-covered filaments in this center region. Additionally, this central stream of higher speed may act to entrain the peripheral streamlines and result in their convergence above the branchial crown.

Crown posture in ambient currents

The filaments of the branchial crown of *E. vancouveri* are arranged in two lateral spirals of equal size (Banse, 1979). When the worm emerges from its tube these paired whorls of filaments unfurl and fill a volume above the tube that is like a rounded cone or pointed hemisphere in shape. Each filament describes an arc, with the pinnules on the upper or oral surface (Fig. 1A). In still water, the branchial crown is positioned symmetrically over the tube, with the plane of the base of the crown perpendicular to the long axis of the tube (Fig. 1B).

In flowing water, 10 to 40 cm/s, the apex of the crown is angled downstream. In this position the leading edge of the crown is raised and the plane of the base of the crown is no longer perpendicular to the long axis of the tube (Fig. 1C). The spiral tiers of the crown intersect the ambient flow at approximately 30° to 40°. This orientation of suspension feeding structures is known for a wide variety of animals (Warner, 1977). The paths of natural particles and fluorescein dye streams around the branchial crown in this orientation indicate that there is a downstream eddy into which the pinnules of the filaments project. At higher speeds (above 40 cm/s), the worms partially withdraw into their tubes, drawing the filaments of the crown together.

Flow patterns in the field

The distribution of flow velocities around a cluster indicates that the cluster acts as a semi-porous barrier or breakwater, causing the bulk of water in a passing wave to flow over the surfaces of the cluster rather than through the mass of tubes (Table I, Fig. 2). The flow speed is highest at the surface of the cluster where the branchial crowns are positioned. Lower values occur within the cluster, below the surface of the branchial crowns. There is no appreciable change in flow speeds around solitary animals in the same habitat. Thus, animals in clusters experience higher flow at crown level than do solitary animals when both are located in the same habitat.

Particle removal

The total particle depletion during a single wave passage through a cluster ranges from 45 to 65%. Figure 3 gives the size-frequency distribution of particles in a wave before and after passing a worm cluster; Figure 2 illustrates the water sampling locations. There is less than a 9% difference in this value for two waves passing over the same cluster; and less than a 7% difference for duplicate samples taken from the same wave downstream from a cluster. The fraction of particles removed was not constant over all sizes ($\alpha = 0.05$, Kolmogorov-Smirnov; Siegel, 1956). In all cases the lowest percent particle removal was at the large end of the size distribution, above 7 μm . The highest percent removal was between 3 and 6 μm .

DISCUSSION

Two factors have led to potentially erroneous views about the method and degree of success of suspension feeding in the sabellid polychaetes. In the first case, previous

TABLE I

Current speeds around clustered and solitary worms¹

	Mean maximum speed \pm S.D. (N) (cm s ⁻¹) pre-cluster	Mean maximum speed \pm S.D. (N) (cm s ⁻¹) crown level	Mean maximum speed \pm S.D. (N) (cm s ⁻¹) below crowns	Worm density (tubes m ⁻²)	Cluster length parallel to flow (cm)
Cluster 1	11.2 \pm 2.1 (13)	12.7 \pm 1.0 (12)	8.0 \pm 2.2 (13)	1243	50
Cluster 2	23.6 \pm 2.1 (11)	31.8 \pm 1.8 (11)	3.7 \pm 0.8 (13)	2576	150
Cluster 3	27.7 \pm 2.9 (16)	33.6 \pm 2.3 (23)	16.6 \pm 2.7 (17)	2448	50
Solitary worm	8.5 \pm 0.7 (15)	8.5 \pm 1.3 (15)	—	1	—

¹ The placement of probes around clusters is diagrammed in Figure 2.

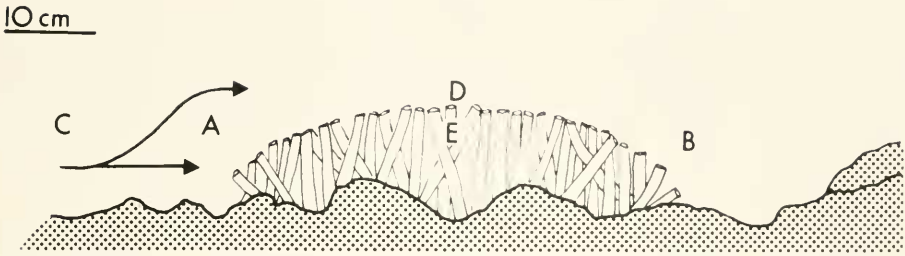


FIGURE 2. Flow and water sampling sites through a section of a cluster of *Eudistylia vancouveri*. (A) Site of pre-cluster water sample removed. (B) Site of post-cluster water sample removed. (C) Site of upstream dye release and velocity measurements. (D) Site of velocity measurements at crown height. (E) Site of below crown velocity measurements. Arrow indicates the direction of flow during water sampling and traces the path of the dye marker during one wave passing through the cluster. Note that the sampling site is in a surge channel and flow is bidirectional. Cluster drawn to scale.

workers (Nicol, 1930; Dales, 1957; Fitzsimmons, 1965; Lewis, 1968; Bonar, 1972; Sorokin, 1973) have not taken into account the importance of ambient water movement in suspension feeding. They have all studied the process in still water, a fluid regime the worms rarely, if ever, experience. However, if the natural flow conditions are considered, it is clear that the velocity of water in contact with and surrounding the branchial crown is two to three orders of magnitude greater than that produced by the cilia alone. Thus, any estimate of feeding that is based on only ciliary currents grossly underestimates the rate at which water and food are processed by the worm. Second, it is important to realize that flow rates *per se* are not the sole criterion by which filtration efficiency should be evaluated. If a suspension feeder can acquire all the food it needs by generating low filtration velocities, it may well be more efficient than suspension feeders that generate high flow rates at greater energetic cost (this latter point is addressed in LaBarbera, 1984).

In ambient flow, the majority of the feeding surface of the crown (the pinnules) is positioned on the downstream side of the worm. The wake of tubes is characterized as an area of relatively slow moving fluid, forming erratic spirals or eddies (Carey, 1983). Warner (1977) suggests that the advantage of positioning particle capture surfaces in this area is that reduced flow speed and chaotic or recirculating particle movement may enhance capture of the particles (also see Meyer, 1973; Rubenstein and Koehl, 1976).

Clusters of *E. vancouveri* remove up to 65% of all particles in a wave washing over them (more than 70% of particles 3 to 6 μm in diameter, Fig. 3). Sabellids are known to filter bacterial cells 0.5 μm in diameter from a suspension of single cells. Only sponges were shown to be as successful at this small size range (Sorokin, 1973). Other suspension feeders (ascidians, bivalves, and calanoid copepods) take larger particles (above 3 to 7 μm in diameter) (Haven and Morales-Alamo, 1970; Sorokin, 1973; Vahl, 1973; Wright *et al.*, 1982). Thus it may be that sabellids are concentrating on the smaller range of plankton composed of bacterio-, myco-, and small phytoplankton, which are readily assimilated (Sorokin, 1973) and constitute the greatest proportion of the planktonic biomass (Sieburth *et al.*, 1978).

The densely packed mounds of tubes of *E. vancouveri* alter the velocity profile of an incoming wave. The thicket of tubes restricts water flow and forces the bulk of the water to travel over the surface of the mound. This flow pattern has two advantages for the worms. The tubes are subjected to lower drag forces (Merz, 1984)

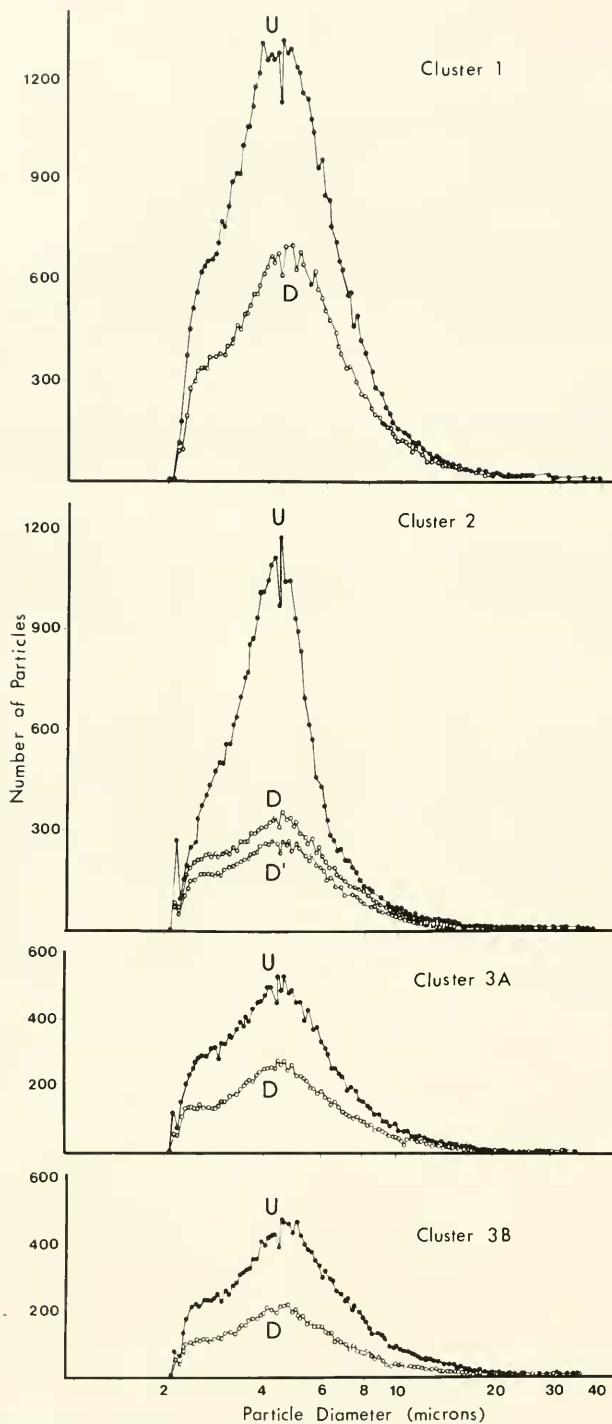


FIGURE 3. Size-frequency distributions for natural suspended particles before and after passing through a worm cluster. In each case line U represents the upstream pre-cluster sample, line D or D' represent the post-cluster sample (see Fig. 2). The results from three clusters are shown. In cluster 2, lines D and D' represent two post-cluster samples taken from the same wave. Cluster 3A, B are measurements of the same cluster for two different waves, 20 minutes apart. (These clusters are not those shown in Table I).

and the feeding crowns are positioned in the fastest flowing water at the surface of the cluster (Fig. 2, Table I) where they are exposed to more water and food per unit time than is a solitary animal (Table I). Koehl (1977) suggests that sessile suspension feeders should minimize drag on their support structure while maximizing flow through their feeding structure. The hemispherical aggregates of *E. vancouveri* accomplish both of these objectives.

Many suspension feeders live with non-clonal conspecifics in hemispherical mounds. For example, sabellid genera contain species that aggregate in this way (O'Donoghue, 1924; Chapman, 1955; Hartman, 1969; Koechlin, 1977), as do some chaetopterid polychaetes (Bailey-Brock, 1979), phoronids (Johnson, 1959; Ronan, 1975), and goose barnacles (Kozloff, 1973). All these animals are either passive suspension feeders or are facultatively active suspension feeders (*sensu* LaBarbera, 1977), and as such depend to some extent on ambient flow for feeding. These animals cluster together into potentially competitive aggregates for several reasons. One may be that domes increase flow through the feeding structures and simultaneously reduce drag on supportive structures. The mound itself forces the bulk of water to flow over the surface. Thus each animal is acting in its own interests, but in so doing contributes to the formation that benefits others in the mound.

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